Probing the Neural Systems Underlying Flexible Dimensional Attention

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Abstract

■ Flexibly shifting attention between stimulus dimensions (e.g., shape and color) is a central component of regulating cognition for goal-based behavior. In the present report, we examine the functional roles of different cortical regions by manipulating two demands on task switching that have been confounded in previous studies—shifting attention between visual dimensions and resolving conflict between stimulus–response representations. Dimensional shifting was manipulated by having participants shift attention between dimensions (either shape or color; dimension shift) or keeping the task-relevant dimension the same (dimension same). Conflict between stimulus–response representations was manipulated by creating conflict between response-driven associations from the previous set of trials and the stimulus–response mappings on the current set of trials (e.g., making a leftward response to a red stimulus during the previous task, but being required to make a rightward response to a red stimulus in the current task; stimulus–response conflict), or eliminating conflict by altering the features of the dimension relevant to the sorting rule (stimulus–response no-conflict). These manipulations revealed activation along a network of frontal, temporal, parietal, and occipital cortices. Specifically, dimensional shifting selectively activated frontal and parietal regions. Stimulus–response conflict, on the other hand, produced decreased activation in temporal and occipital cortices. Occipital regions demonstrated a complex pattern of activation that was sensitive to both stimulus–response conflict and dimensional attention switching. These results provide novel information regarding the distinct role that frontal cortex plays in shifting dimensional attention and posterior cortices play in resolving conflict at the stimulus level. ■

INTRODUCTION

Controlled cognition often involves switching attention between visual dimensions that are relevant in different behavioral contexts. For example, we may attend to the shapes of objects when trying to find bananas in the grocery store but then attend to the color when trying to find ones that are ripe. In such situations, different dimensions (e.g., shape and color) of the same object are associated with different decisions, and attentional processes must select the appropriate dimension for processing and response selection. Previously attended visual information must be ignored, and previously ignored visual information must now be attended. In this way, dimension switching is unique from other types of switching. Task or response switching only requires alternating between different stimulus–response mappings or assigning new responses to the same stimuli (Crone, Wendelken, Donohue, & Bunge, 2006). Thus, these other forms of switching do not require early selection at the level of the stimulus dimension. In this report, we use fMRI with adult participants to examine the neural basis of this form of task switching using a novel implementation of a dimensional attention task that has been extensively used with children.

The Processes Underlying Task Switching

The ability to update behavior is often studied using a task switching paradigm (e.g., Kiesel et al., 2010). In this context, a task consists of a set of stimulus–response mappings indicating the motor actions (e.g., pressing a button) that should be made in response to a set of stimuli. Switch costs are typically observed in the form of longer RTs when switching to a new task compared to repeating the same task. These switch costs are typically thought to reflect the additional time needed to activate the new task in working memory. Furthermore, the relationship between the two tasks can impact the magnitude of switch costs. For example, if the tasks pair different responses with the same stimuli, then larger switch costs are observed compared to switching between two tasks that use different sets of stimuli. Stimuli that have response mappings for two tasks are bivalent and impose additional inhibitory demands because of the stimuli being mapped to multiple response options.

Task switching can also involve shifting attention to visual features of different dimensions of the same set of stimuli. For example, one task may instruct responses

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to the colors of a set of objects and the other task may instruct responses to the shapes of the same set of objects. In this case, the stimuli are bivalent because they are mapped to two sets of responses, but also require dimensional attention to select the information along the dimension that is relevant for the current task. Consider the dimensional change card sort (DCCS) task shown in Figure 1. The DCCS task explicitly cues the need to shift dimensional attention by instructing participants to match objects based on shape or color. *Target* objects and arrow types in the left panel of Figure 1 show the response mappings for the shape or color rules for each *test* object. For instance, the wavy green *test* object in the upper left corner of this panel should be matched to the left green *target* object in the color game (see dotted arrow), whereas this same *test* object should be matched to the right wavy orange *target* object in the shape game (see solid arrow). Note that the to-be-sorted *test* objects match either *target* object along different dimensions, creating visual conflict and forcing the selection of the relevant dimension. The right panel of Figure 1 shows how the task unfolds over trials. First, a dimensional cue is presented (see "c" for the color game) along with the two target objects in the lower portion of the display. Next, the dimensional cue disappears, and a test object is presented centrally in the upper panel. The participant must then press a button to indicate the target object to which the test object should be sorted—the left green *target* object in this case. This is followed by the next trial that starts with the presentation of either the same or different target cards and/or the same or a different dimensional cue. Switch costs are typically observed in the form of longer RTs when shifting dimensions (e.g., a *color* sorting trial preceded by a *shape* sorting trial) compared to repeating dimensions (e.g., a *color* sorting trial preceded by a *color* sorting trial; Morton, Bosma, & Ansari, 2009; Diamond & Kirkham, 2005).

Although the DCCS task has only been used to a limited degree with adults, literature on executive function development sheds light on the unique processes that underlie dimensional attention switching in this task. The DCCS task is popular in the developmental literature because it reveals a qualitative improvement in performance: 3-year-olds predominantly fail to switch rules, but most 4-year-olds have little difficulty switching (Zelazo et al., 2003). Thus, this task is often used as a measure of the developmental status of executive function. The widespread use of this task with children has resulted in numerous variations, some of which improve switching in young children. Thus, the pattern of success or failure with children indicates which factors of the task create challenges to dimensional attention switching.

Two characteristics of the stimulus–response representations that impact dimensional switching in this task are illustrated in Figure 2. The top shows the configuration of test objects and target objects with lines showing the test-to-target mappings as in Figure 1. Notice that the visual structure of the task primes conflicting responses for each test object. For example, the wide-green test object matches the leftward target object by color but matches the rightward target object by shape. This visual conflict matters: If target objects are not used in the task and rules are simply provided verbally, then young children have little difficulty switching (Towse, Redbond, Houston-Price, & Cook, 2000). The primary challenge of the DCCS is not task switching itself, but the need to use dimensional attention to map the features of the test objects to the features on the target objects.

To illustrate the dynamics of neural representations of the features involved in this task, we use the schematic representation in the lower panels of Figure 2. The solid line bumps in the bottom shows the "activation" in feature-encoding neural populations created by viewing the target objects in particular spatial positions. Thus, the green target object on the left generates a bump of activation on the left side of the color representation at the green value, and on the left side of the shape representation at the "less wavy" spatial frequency value. By

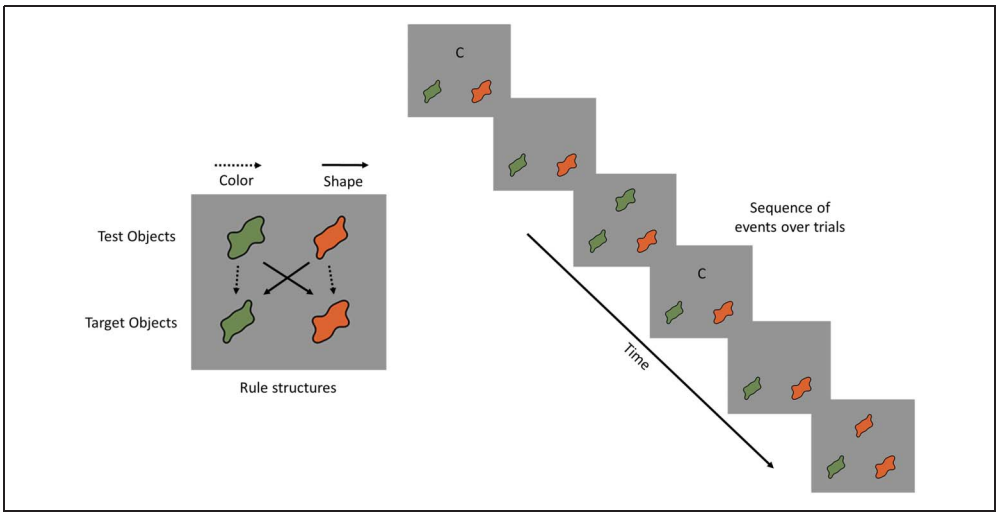

Figure 1. Left: Depiction of the standard DCCS task. Target objects show which features go to which response location for the shape or color rules. Test objects match either target object along different dimensions. Right: Depiction of sequence of events over two trials.

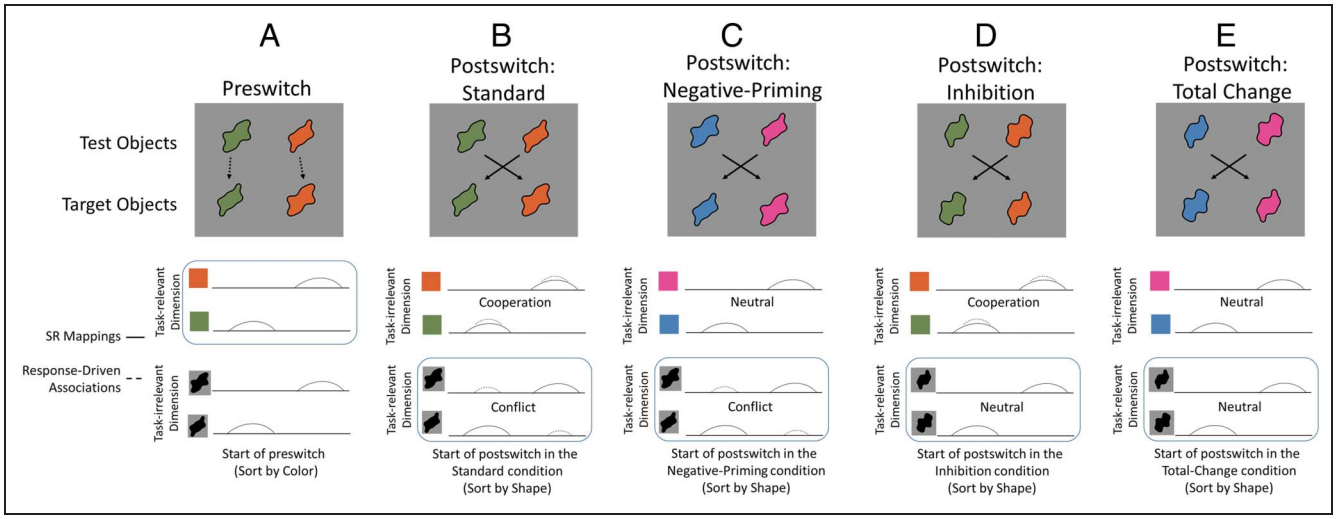

Figure 2. Depiction of stimulus–response representations across different variations of the DCCS task (see also Table 1). Lines illustrate the strength of input being contributed by the stimulus–response (SR) mappings (solid) and response-driven associations (dashed). In this example, color is the preswitch dimension and shape is the postswitch dimension.

contrast, the orange target object on the right generates a bump on the right side of the color representation at the orange value, and on the right side of the shape representation at the "more wavy" spatial frequency.

The dashed bumps in the lower panels of Figure 2 capture the second important characteristic of stimulus–response representations in this task—response-driven associations that build up over trials (dashed lines). Figure 2A shows a preswitch phase in which the rules are to sort by color. Note that there are no response-driven association bumps in the lower stimulus–response representations because there is no prior history with the task. Over trials (moving from Figure 2A to 2B), stimulus–response associations form between the responses and the features of both the relevant and irrelevant dimensions of the test objects. In particular, Figure 2B shows the status of stimulus–response representations at the start of the postswitch phase in the standard DCCS task. Because the "more wavy" green test object was sorted to the left in the preswitch phase (see Figure 2A), there is a dashed activation bump on the left at the green feature value and also a dashed bump on the left at the "more wavy" spatial frequency. Similarly, there is a dashed bump on the right at the orange feature value and a dashed bump on the right at the "less wavy" spatial frequency. Notice that this leads to a pattern of "cooperation" in the color-response representation because the solid and dashed bumps overlap, and a pattern of "conflict" in the shape–response representation because the solid and dashed overlap with opposite response. In the context of dimensional switching, this means that the preswitch dimension—color—is primed by the cooperation whereas the postswitch dimension—shape—experiences inhibitory competition based on this conflict.

Evidence that these response-driven associations impact performance in the DCCS task comes from multiple studies (see Table 1 for a summary). In a negative priming version of the task (Figure 2C), the features that were relevant during the preswitch phase (e.g., Figure 2A) are altered before the start of the postswitch phase. For instance, in Figure 2C, the features of the color dimension are changed in both the target and test objects. Consequently, response-driven associations are no longer present in the color-response representation (note the absence of dashed lines in the "neutral" color representation of Figure 2C). In this condition, the majority of young children still perseverate (Buss & Spencer, 2014; Müller, Dick, Gela, Overton, & Zelazo, 2006; Zelazo et al., 2003) because of the conflict that remains within the shape–response representation (see Figure 2C). Thus, even though the stimulus–response mapping that was relevant during the preswitch phase is no longer relevant because those features are now absent from the stimuli, young children still fail to switch rules. On the other hand, children also perseverate in an inhibition version (Zelazo et al., 2003) of the task in which the features of the dimension that is being switched to are altered before the start of the postswitch phase (see Figure 2D). In

Table 1. Summary of Conditions Used with Children in the DCCS Task and the Task Factors That Have Been Manipulated

	Irrelevant Dimension	*Relevant Dimension*	*3-year-old Behavior*
Negative-priming	Neutral	***Competition***	Perseverate
Inhibition	***Cooperation***	Neutral	Perseverate
Total change	Neutral	Neutral	Switch
No-conflict	Cooperation	Cooperation	Switch

The **bold** and underlined factors in the table highlight the factors that drive perseveration in 3-year-olds.

this case, the "cooperative" stimulus–response associations that remain along the features of the preswitch dimension (i.e., color in Figure 2D) interfere with the ability to use the features of the postswitch dimension (i.e., shape) to make sorting decisions.

Importantly, the majority of young children can switch rules in a total-change version (Zelazo et al., 2003) in which the features of both dimensions are changed before the start of the postswitch phase (see Figure 2E). Note that the dashed bumps reflecting the learned stimulus–response associations from the preswitch phase are absent ("neutral") for the features of both dimensions. In the absence of any influence of stimulus–response associations from the previous sorting phase, young children have little difficulty switching rules. Together, these results indicate that the object features that are irrelevant for the current sorting rules are nonetheless bound to responses, and the status of stimulus–response representations across both the relevant and irrelevant dimensions impacts the ability to shift dimensional attention.

In summary, the DCCS presents unique challenges in the context of dimensional task switching. The task requires dimensional attention, which is an additional level of visual processing beyond the stimulus identification required in other response selection tasks. In addition, the binding of features across stimulus dimensions leads to the formation of stimulus–response associations that also includes task-irrelevant features. Beyond early childhood, however, it is unclear whether such bindings occur or how they might influence dimensional attention.

Neural Basis of Task Switching

Neuroimaging research has identified a network of frontal and parietal regions that are engaged in response to demands on task switching. This network includes dorsolateral prefrontal cortex, pre-SMA, dorsal premotor cortex, inferior frontal junction, anterior insula cortex, and posterior parietal cortex (Cole & Schneider, 2007). Moreover, some regions are sensitive to the relationship between tasks. SMA and pre-SMA are more strongly activated for bivalent compared to univalent rules, and ventrolateral prefrontal cortex is more strongly activated when switching to bivalent rules (Crone et al., 2006). Data from studies using the DCCS task have identified a similar network composed of inferior and dorsal frontal cortex, parietal cortex, and thalamus that is more strongly activated when switching dimensions compared to repeating the same dimension (Morton et al., 2009). This research also suggests that distinct neural mechanisms may be involved in dimensional attention shifting. Specifically, switch-related activity has been identified in fusiform cortex, a region not previously implicated in task switching (Morton et al., 2009). Fusiform cortex is involved in object representation processes and is modulated by attentional signals that prioritize processing of specific perceptual information (Tallon-Baudry, Bertrand, Hénaff, Isnard, & Fischer, 2005; Liu, Slotnick, Serences, & Yantis, 2003; Clark et al., 1997). Lastly, electrophysiological data have demonstrated dissociable electrophysiological signatures of processing demands in the DCCS. Specifically, central frontal N2 amplitude is greater for bivalent compared to univalent test objects, whereas frontal negativity was associated with the magnitude of costs when switching dimensions (Waxer & Morton, 2011).

Developmental neuroimaging studies using the DCCS converge with these patterns of results for task switching and dimensional attention switching. Children demonstrate increased activation within frontal, parietal, and temporal cortex as the ability to switch rules develops (Buss & Spencer, 2018; Moriguchi & Hiraki, 2009). In addition, this literature sheds light on the influence of conflict between learned stimulus–response associations and stimulus–response mappings for a given task. Specifically, this research examined neural activation during a no-conflict negative priming version of the DCCS illustrated in Figure 3. As shown in Figure 3A, the preswitch phase of the task is modified so that the test cards match the target cards along both dimensions. That is, a "less wavy" green test object is sorted to a "less wavy" green target object and the "more wavy" orange test object is sorted to a "more wavy" orange target object. Standard test objects that contain visual conflict are used during the postswitch phase. The primary influence of this manipulation is to create stimulus–response associations that cooperate with the stimulus–response mappings required for the postswitch phase. In the absence of conflict, stronger activation is observed in parietal and temporal regions (Buss & Spencer, 2018) suggesting that posterior object representation areas are sensitive to the conflict between response-driven associations from the previous task and stimulus–response mappings for a current task.

Current Study

Developmental studies have revealed that stimulus–response conflict (SC) plays a distinctive role in children's ability to switch rules in dimensional attention tasks. Both the relevant and irrelevant features matter, suggesting that rule-use is not selectively focused on the task-relevant dimension but instead integrates across all object features. In previous fMRI studies that have used the standard DCCS task, conflict at the level of dimensional attention created by switching from one dimensional rule to another is confounded with SC. Given that recent neuroimaging results with children demonstrate that switching dimensions and resolving SC have different influences on the functioning of frontal and posterior brain regions, our goal in this study was to clarify the roles of different brain regions in shifting dimensional attention.

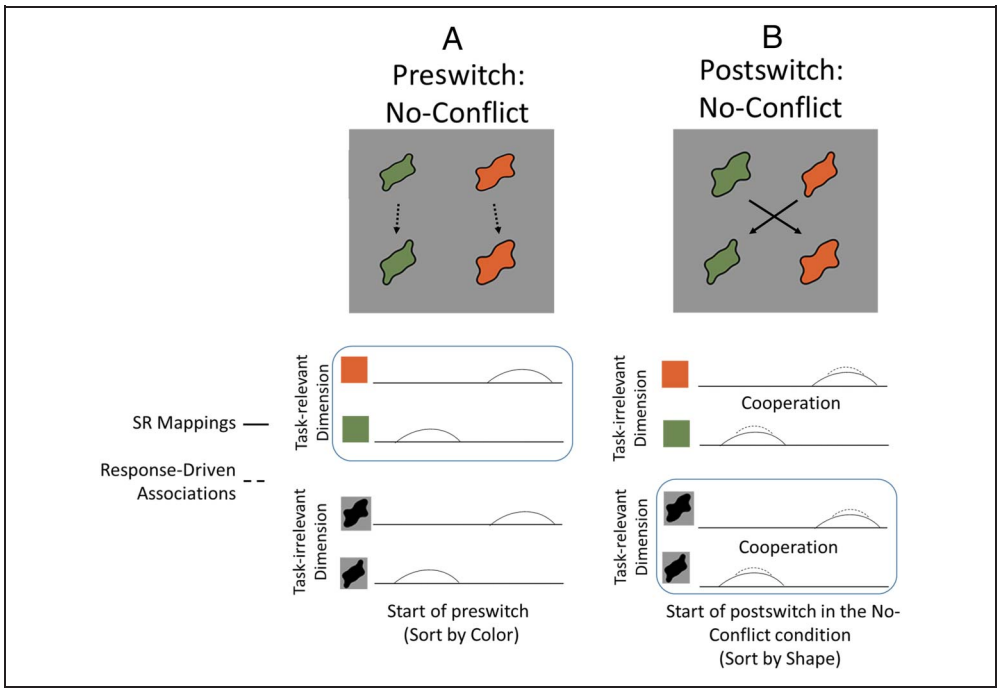

Figure 3. Depiction of stimulus–response representations in the no-conflict version of the DCCS.

The goal of the current study is to independently manipulate the status of stimulus–response representations and dimensional shifting while collecting functional MRI with adults. As discussed above, stimulus–response representations in the context of the DCCS task are important to consider along both the task-relevant and task-irrelevant dimensions. Thus, to manipulate the status of stimulus–response representations, both aspects must be considered and controlled. In this study, we focus on SC with regard to the features that are relevant for the current phase of sorting; stimulus–response representations involving the features that are irrelevant for the current phase of sorting was held constant across conditions. In particular, the stimulus–response associations always cooperated with the target stimuli features within the task-irrelevant dimension (i.e., the location of the task-irrelevant features on the target objects always overlapped with the locations where those features were sorted during the previous phase as illustrated along the color dimension in Figures 2B). Note that this is a property of the standard DCCS task.

To manipulate SC along the task-relevant dimension, we either kept the same features between the pre- and post-switch phases or we changed the features along the post-switch dimension. If the features were not altered, then the current stimulus–response mappings conflicted with the stimulus–response associations from the previous task. That is, participants had to make responses to the task-relevant features that were the opposite of the responses made to those features in the previous phase (SC), as in the standard DCCS task (illustrated along the shape dimension in Figure 2B). If the relevant features changed, then there were no stimulus–response associations from the previous phase for those features and there was no SC along the relevant dimension (stimulus–response no-conflict [SN]), as in the inhibition version (illustrated along the shape dimension in Figure 2D).

We also manipulated the need to shift attention between visual dimensions. Specifically, conditions either required participants to shift attention to the other dimension (dimension change [DC]) or to reverse the stimulus–response mapping for features within the same dimension (dimension same [DS]). When shifting dimensions, participants were instructed to shift from sorting by shape to sorting by color, or vice versa. If participants were to reverse the stimulus–response mappings, then participants were cued to continue sorting by the same dimension, but the target objects would swap locations, indicating a set of stimulus–response mappings. Thus, in both cases, there was a change that required a new mapping of the stimuli to response locations.

These manipulations created four conditions (see Table 2): dimension change/stimulus–response conflict (DCSC), dimension change/stimulus–response no-conflict (DCSN), dimension same/stimulus–response conflict (DSSC), and dimension same/stimulus–response no-conflict (DSSN). The DCSC condition is the standard condition from the literature (Morton et al., 2009; Zelazo

Table 2. Factors Manipulated across Conditions in the Behavioral Task

	Stimulus-Response Conflict	*Stimulus-Response No-Conflict*
Dimension Change	DCSC	DCSN
Dimension Same	DSSC	DSSN

Note that switch and repeat trials were included for all conditions.

et al., 2003). The DCSN is the inhibition condition from the literature (Zelazo et al., 2003). The DSSC and DSSN are novel conditions that have not been used in previous studies. Previous fMRI research has only examined the DCSC condition.

Our task was administered in an alternating runs design in which participants were given three trials (TR1, TR2, and TR3) for each condition before transitioning to the next condition. Based on previous studies, we can outline a set of predictions regarding the pattern of activation across different conditions. First, we expect switch trials (the first of the three trials) to elicit stronger activation relative to repeat trials (the subsequent two trials) in frontal and parietal regions previously implicated in dimensional attention as well as object representation regions in temporal cortex (Buss & Spencer, 2018; Morton et al., 2009). Second, we expect stronger activation in frontal and parietal regions for DC conditions compared to DS conditions. Third, based on the hemodynamic data reported by Buss and Spencer (2018), we expect stronger activation in parietal and temporal cortices when SC is absent compared to when conflict is present along the task-relevant dimension. In summary, we expect manipulations of the demands on shifting attention to a new dimension to produce activation differences in frontal and parietal cortices and manipulations of task-relevant feature conflict to produce activation differences in object representation areas in temporal and parietal cortices.

METHODS

Participants

Twenty adults (M_{age} = 23.8 years, SD = 3.8 years; nine men) were enrolled into this study after providing informed written consent in accordance with the local institutional review board. Monetary compensation was provided to the subjects for their participation. All participants were right-handed and reported normal or corrected-to-normal vision. The data were collected as part of a larger six-session fMRI study. The DCCS sessions presented here were collected over four half-hour sessions. Each session included two runs that were composed of 123 trials, which lasted for 12 min each.

Behavioral Procedure

The study used a continuous event-related design with interleaved phases, similar to other task switching paradigms that use alternating runs (e.g., Rogers & Monsell, 1995). Participants were not informed about this aspect of the task. Participants were instructed to match the object presented at the top of the screen to responses indicated by the location of target objects at the bottom of the screen. A dimensional cue of the letter "C" or "S" was presented at the start of each trial to indicate which dimension was relevant for the upcoming trial. Colors were sampled from CIE Lab color space (see Figure 4). Shape stimuli were generated from a continuous space defined by the phase angle of Fourier components (Drucker & Aguirre, 2009; Zahn & Roskies, 1972; see Figure 4). This allows the metric details of shape to be controlled in a similar fashion as color. The objects used in the task were approximately 60 × 60 pixels and consisted of a black outline filled with color.

The bottom of Figure 4 shows the sequence of events on a given trial. Each trial began with an "S" or "C" presented in the upper center of the screen to indicate whether to match by shape or color on the upcoming trial, and the target objects were presented to the left and right on the lower portion of the screen. After 1000 msec, the dimensional cue was removed and replaced with an "X." After 1500 msec, the "X" was replaced with a test object. Target object and test objects were approximately 2° of visual angle. Participants were given 1500 msec to press a button with their right index or middle finger, mapping onto a leftward or rightward sorting response. If a response was not produced during this time window, a warning appeared on the screen telling the participant to respond more quickly. The duration between the end of a trial and the beginning of a subsequent trial was jittered at 1500, 3000, or 5000 msec in a 2:1:1 ratio, respectively.

Figure 5 illustrates the different conditions used in the experiment by showing an example of the stimulus presentation phase across a sequence of trials (see also Table 2) and the different task factors present for each condition. In the bottom, task inputs are plotted in solid lines and correspond to the locations of inputs in the target images. Memories accumulated from the previous phase of sorting are plotted in dashed lines. The features that are relevant for each phase of sorting are outlined in the box. Each panel in Figure 5 illustrates an example of stimuli used for a sorting phase, each of which consisted of three trials. The first panel shows stimuli presented during the first three-trial phase of sorting. This is called

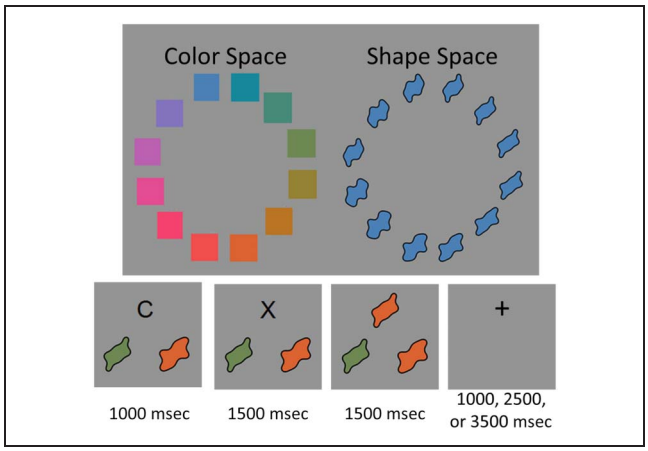

Figure 4. Stimuli and sequence of events in a trial used in the behavioral task.

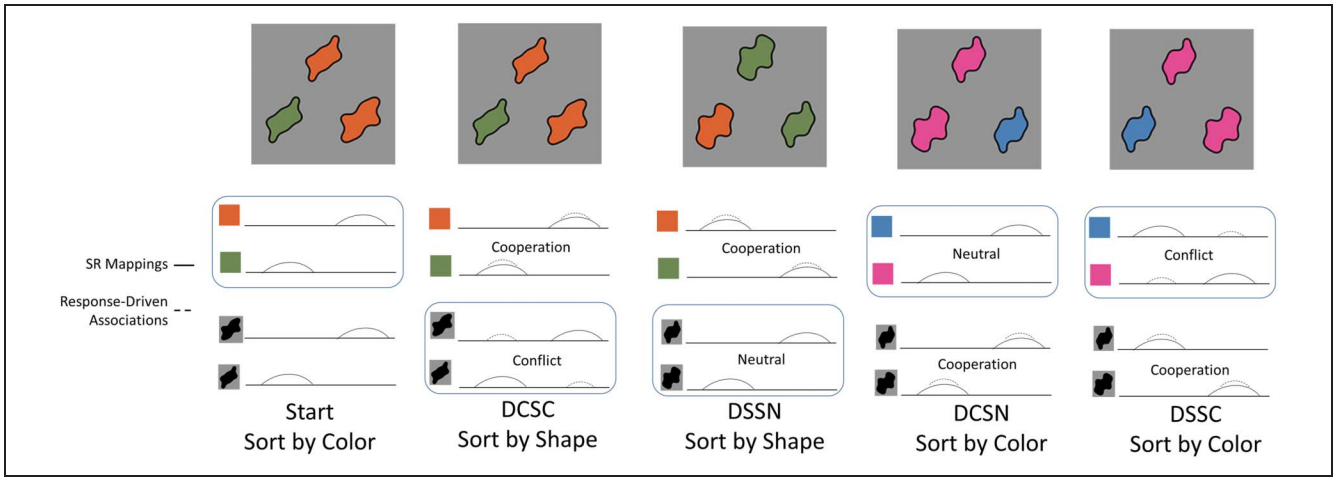

Figure 5. Example sequence of stimuli to illustrate the conditions used in the behavioral task. See Table 2 for details on factors manipulated across conditions. Full sequence was Start (color), DCSC (shape), DSSN (shape), DCSN (color), DSSC (color), DCSN (shape), DSSC (shape), DCSC (color), DSSN (color), DCSN (shape), DSSC (shape), DCSN (color), DSSC (color), DCSC (shape), and so forth.

the Start phase. In this phase, there is no previous task and no memories from a previous sorting phase. The next panel shows the DCSC condition. Here, the relevant dimension switches from color to shape, the features remain the same, and the spatial orientation of the target cards remains the same. Thus, the DCSC condition requires participants to shift attention to a new dimension and resolve SC between stimulus–response associations from previous sorting decisions and the current stimulus–response mapping. The next panel shows the DSSN condition. Here, the relevant dimension stays with shape, the features for the relevant dimension (shape in this example) change to new feature values, and the target objects swap locations. Thus, in the DSSN condition, participants need to establish a new stimulus–response mapping of the task within the dimension that was previously relevant but do not have to overcome SC. The next panel shows the DCSN condition. Here, the relevant dimension switches (in this example from shape to color), the features that are relevant for this phase (color) are changed to new values, and the spatial orientation of the target cards remain the same. Thus, the DCSN condition requires participant to shift attention between dimensions but does not require resolving SC. Finally, the last panel illustrates the DSSC condition. In this condition, the relevant dimension stays the same (color in this example), the features in the task remain the same, and the target images swap spatial locations. Here, participants do not need to shift attention to a new dimension but must resolve SC by reversing the stimulus–response mappings that were used during the previous phase.

Participants completed 10 phases of each condition (counterbalancing shape and color) in each of four total runs, completing a total of 40 phases for each condition. The order of conditions was the same for every run, but the dimensions were the opposite from one run to the next. Features were randomly selected from the array at the beginning of each phase. Each set of features used during any phase were six steps apart. When features changed, they shifted either three or four steps in the feature space (this was randomly selected each time the features changed).

fMRI Data Collection and Analysis

The fMRI study used a 3T Siemens TIM Trio system with a 12-channel head coil. Anatomical T1-weighted volumes were collected using and magnetization prepared rapid gradient echo sequence. Functional BOLD imaging was acquired using an axial 2-D echo-planar gradient echo sequence with the following parameters: echo time = 30 msec, repetition time = 2000 msec, flip angle = 70°, field of view = 240 × 240 mm, matrix = 64 × 64, slice thickness/gap = 4.0/1.0 mm, and bandwidth = 1920 Hz/pixel. Preprocessing and statistical analyses were conducted in AFNI version 17.3.07 (Cox, 1996). Standard preprocessing was used that included slice timing correction, outlier removal, motion correction, and spatial smoothing (Gaussian FWHM = 5 mm). Data were transformed into Montreal Neurological Institute space using a nonlinear transform to warp the data to the common coordinate system. The T1-weighted images were used to define the transformation to the common coordinate system. First-level analysis was performed using multiple linear regression, which included regressors for trial repetition (TR1, TR2, TR3), dimension (same/change), and SC (conflict/no-conflict), as well as motion parameters and baseline parameters (polort = 6) as nuisance regressors.

A 3 × 2 × 2 ANOVA was conducted to contrast effects of switching dimensions (Dimension: change/same), the effects of SC (SC: conflict/no-conflict), and switching versus repeat trials (Trial Repetition: TR1, TR2, TR3). The ANOVA was corrected for multiple comparisons using *3dClustSim* and an estimated autocorrelation function to control for false-positive rates (NN2, voxelwise p = .01, and alpha =.01; Cox, Chen, Glen, Reynolds, & Taylor,

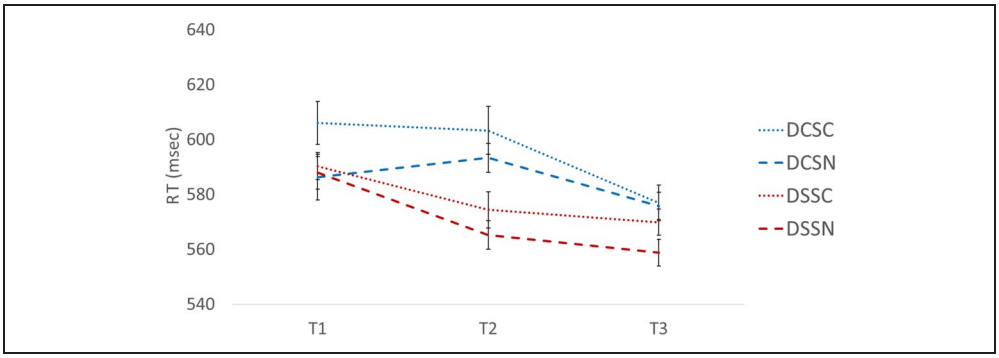

Figure 6. RTs for the three trials in a sorting phase. Error bars represent within-subject error based on Cousineau (2005).

2017). The minimum volume for a cluster was 2672 mm^3 (334 voxels).

RESULTS

Behavioral Results

Figure 6 plots the average RTs across the three trials of each condition. A 2 (Dimension: change, same) × 2 (SC: conflict, no-conflict) × 3 (Trial: TR1, TR2, TR3) ANOVA revealed a main effect of Dimension, $F(1, 19) = 20.5$, $p < .001$, $\eta_p^2 = .519$, with participants performing slower when the dimension changed ($M = 590$ msec) compared to when the dimension remained the same ($M = 574$ msec). The ANOVA also revealed a main effect of SC, $F(1, 19) = 5.4$, $p = .032$, $\eta_p^2 = .220$, with responses being faster when conflict was absent ($M = 578$ msec) compared to when conflict was present ($M = 587$ msec). The ANOVA also revealed a main effect of Trial Repetition, $F(2, 18) = 8.8$, $p = .001$, $\eta_p^2 = .316$. A simple effects test revealed that Trial 1 RT ($M = 593$ msec) was not different from Trial 2 RT ($M = 584$ msec; $p = .526$), but was significantly slower than Trial 3 RT ($M = 570$ msec; $t(18) = 4.083$, $p < .001$). In addition, Trial 2 RT was significantly slower than Trial 3 RT, $t(18) = 3.130$, $p = .006$. Thus, participants performed more quickly over the series of three trials in each block.

Finally, the ANOVA revealed an interaction between Dimension and Trial Repetition, $F(2, 18) = 3.7$, $p = .035$, $\eta_p^2 = .161$. Simple effects tests on the dimension-change conditions revealed that Trials 1 ($M = 596$ msec) and 2 ($M = 598$ msec) were not different from one another ($p = 1.00$), but Trial 3 ($M = 576$ msec) was significantly faster than both Trial 1 ($p = .034$) and Trial 2 ($p = .006$). When the dimension remained the same, Trial 1 ($M = 589$ msec) was marginally slower than Trial 2 ($M = 570$ msec; $p = .056$) and significantly slower than Trial 3 ($M = 564$ msec; $p = .001$). Trial 2 was not different from Trial 3 ($p = 1.00$). Thus, switch costs persisted for two trials when the dimension changed, but switch costs were

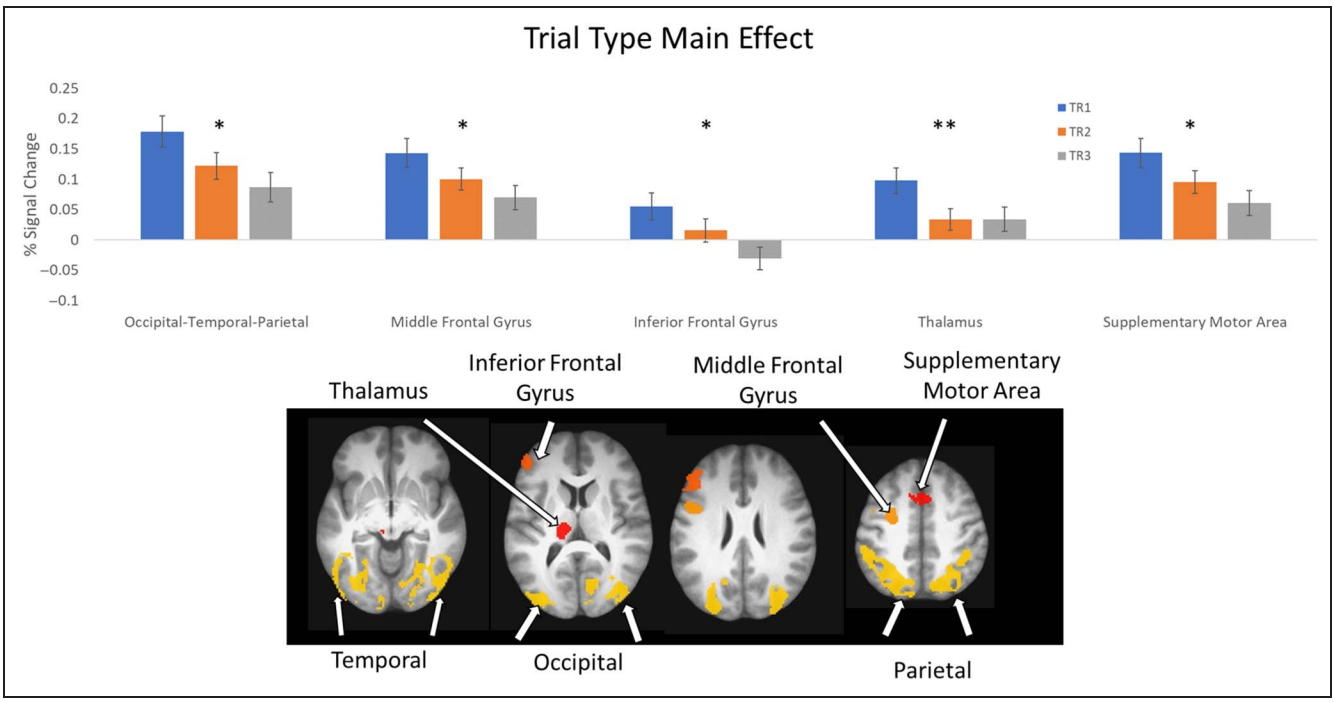

Figure 7. Trial Repetition main effect. Top: average percent signal change within ROIs showing a main effect of Trial Repetition (* indicates TR1 > TR2 > TR3; ** indicates TR1 > TR2 only). Error bars represent standard error of the mean. Bottom: locations of ROIs. See Table 3 for list of ROIs.

Table 3. Clusters of Activation Revealed by the ANOVA

		MNI Coordinates (RAI; mm)				
Region	*Hemi*	*x*	*y*	*z*	*Volume (mm^3)*	*Effect Size*
Trial Repetition Main Effect						
Occipital–temporal–parietal	B	37	55	−21	92,904	.0397
Middle frontal gyrus	L	29	1	51	8,120	.0377
Inferior frontal gyrus	L	51	−49	9	5,656	.0392
Thalamus	L	19	31	−1	3,400	.0512
SMA	B	−5	−13	49	2,400	.0490
Dimension Main Effect						
Inferior parietal cortex	L	33	53	43	15,008	.0306
SMA	B	53	−33	25	7,504	.0306
Inferior frontal gyrus	L	3	−13	51	6,720	.0390
Inferior frontal gyrus	R	−35	−29	−5	4,736	.0416
Insula lobe	L	29	−21	11	3,752	.0307
Superior frontal gyrus	L	11	−45	39	3,504	.0432
Intraparietal sulcus	R	−17	65	43	2,992	.0274
Feature-Conflict Main Effect						
Fusiform gyrus	L	29	39	−15	4,048	.0260
Dimension × Trial Repetition Interaction						
SMA	B	9	−7	59	8,016	.0175
Postcentral gyrus	L	37	31	61	5,480	.0317
Precuneus	L	5	73	47	2,944	.0208
Intraparietal sulcus	L	37	51	41	2,776	.0135
Dimension × Feature-Conflict Interaction						
Inferior occipital gyrus	L	43	83	−5	12,608	.0158
Angular gyrus	R	−29	57	−11	3,592	.0223
Dimension × Feature-Conflict × Trial-Repetition Interaction						
Fusiform gyrus	R	−29	47	−19	9,968	.0184
Middle occipital gyrus	L	23	95	−3	4,024	.0128
Fusiform gyrus	L	35	53	−17	3,688	.0163

MNI = Montreal Neurological Institute; RAI = right anterior inferior.

resolved after a single trial when the dimension remained the same. Recall that, on our DS trials, participants still performed a task switch that involved updating the response mapping for the relevant features. No other significant interactions were observed. Comparing between levels of dimension, Trial 1 RT was not different for the DC (M = 596) and DS (M = 589) conditions (p = .324), but was different on Trial 2 (M = 598 vs. M = 569, respectively; p < .001) and Trial 3 (M = 576 vs. M = 564, respectively; p = .044). Thus, performance was not different on the

initial trial of conditions in which the dimensions changed or remained the same, but differences emerged over the repetition trials.

fMRI Results

We analyzed the fMRI data with a 3 (Trial Repetition: TR1, TR2, TR3) × 2 (Dimension: change vs. same) × 2 (SC: conflict vs. no-conflict) ANOVA. We performed hierarchical clustering so that voxels that were involved in higher-level interactions were ignored when examining lower-level interactions or main effects. Figure 7 shows results for clusters with a significant main effect of Trial Repetition. Note that this is the first direct comparison of switch versus repeat trials in this task; previous studies (Ezekiel, Bosma, & Morton, 2013; Morton et al., 2009) performed a contrast between switch blocks and repeat blocks. Consistent with these previous attention switching studies, stronger activation was observed on switch trials compared to repeat trials for all clusters. A large cluster was observed that spanned from bilateral fusiform cortex through inferior temporal, occipital, and parietal regions. Additional localized clusters were observed in middle and inferior frontal gyri, thalamus, and SMA (see Table 3 for details). Except for the thalamus, these regions showed decreases in activation across all TRs

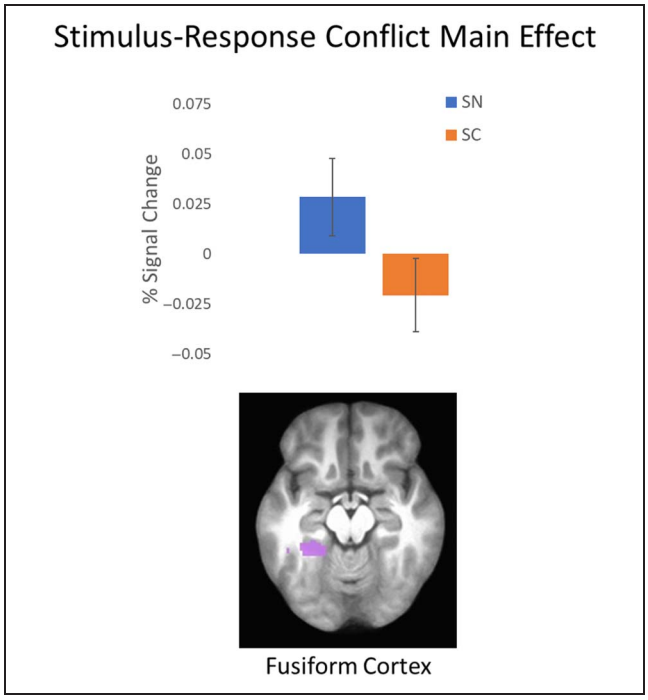

Figure 9. SC main effect. Top: average percent signal change from the ROI showing a main effect of SC. Error bars represent standard error of the mean. Bottom: location of ROI. See Table 3 for details of ROI. SC = stimulus–response-conflict.

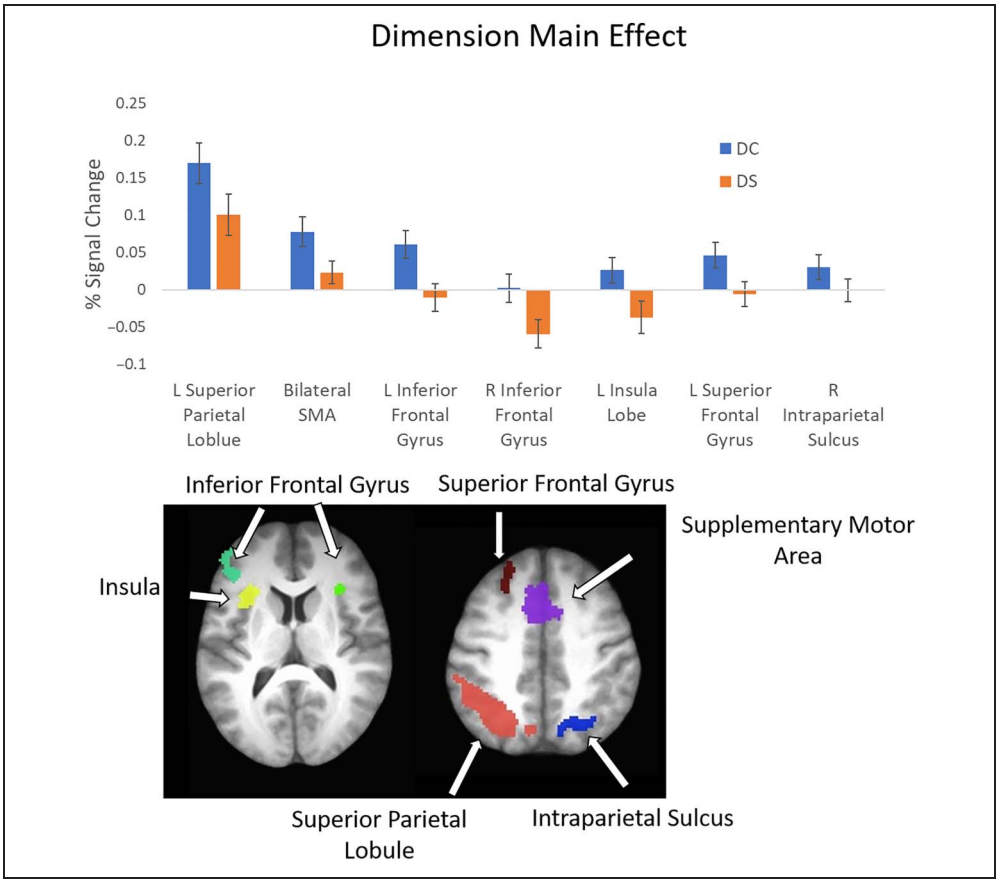

Figure 8. Dimension main effect. Top: average percent signal change from the seven ROIs showing a main effect of dimension. Error bars represent standard error of the mean. Bottom: locations of ROIs. See Table 3 for list of ROIs.

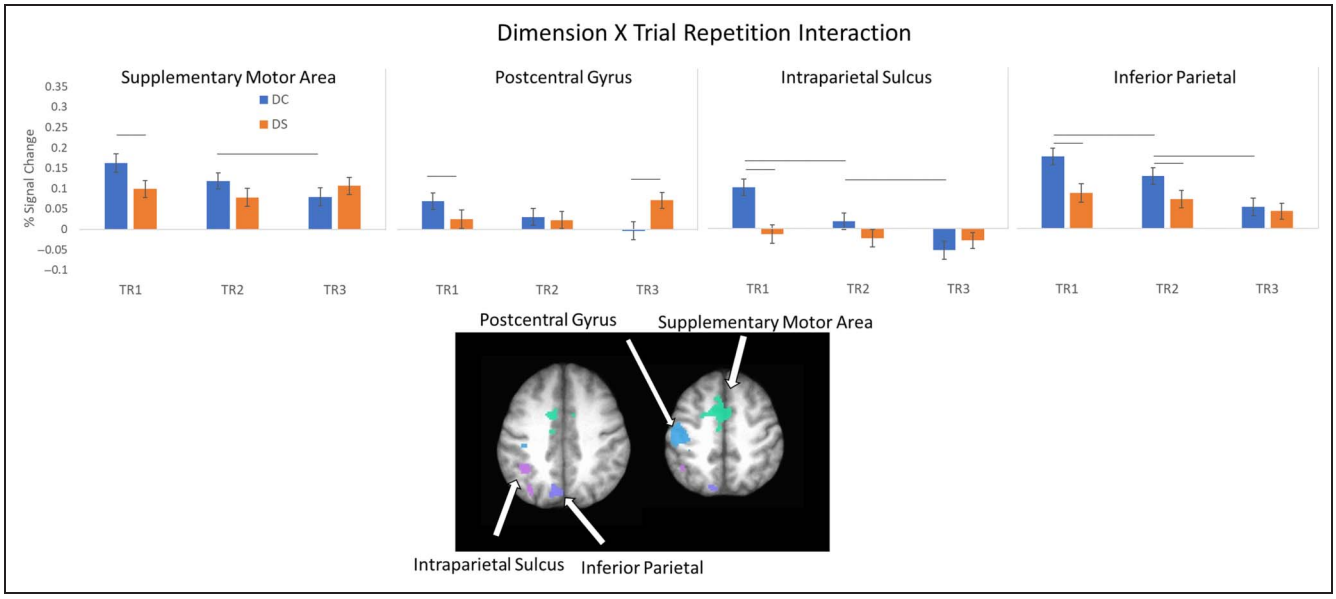

Figure 10. Dimension × Trial Repetition interaction. Top: average percent signal change from the ROIs showing an interaction between dimension and trial repetition. Error bars represent standard error of the mean. Bottom: location of ROI. See Table 3 for list of ROIs.

(all $p < .003$). Activation in thalamus decreased from TR1 to TR2 ($p < .001$) but was not different between TR2 and TR3 ($p = .968$). Thus, switching was associated with activation a distributed network that spanned regions of frontal, parietal, and temporal cortices and subcortex.

Next, we examined the main effect of Dimension (Figure 8). This is the first examination of rule switching that involves shifting dimensions compared to not switching dimensions. This contrast revealed differences in activation across frontal and parietal regions (see Table 3 for details). Consistent with the predictions outlined above, stronger activation was observed when the relevant dimension changed compared to when it remained the same within all activated clusters (see bar plot in Figure 8). Examining the main effect of SC, one cluster was detected in the left fusiform gyrus (see Figure 9 and Table 3). Consistent with findings from Buss and Spencer (2018), activation was stronger in this cluster when SC was absent.

An interaction was observed between Trial Repetition and Dimension in left SMA, postcentral gyrus, intraparietal sulcus, and inferior parietal cortex (see Figure 10). Within each cluster, seven follow-up tests were conducted to compare adjacent trials within a condition (TR1 vs. TR2, TR2 vs. TR3) and between conditions for each TR. Threshold values were adjusted using Bonferroni–Holm corrections. In left SMA, activation on TR2 was significantly

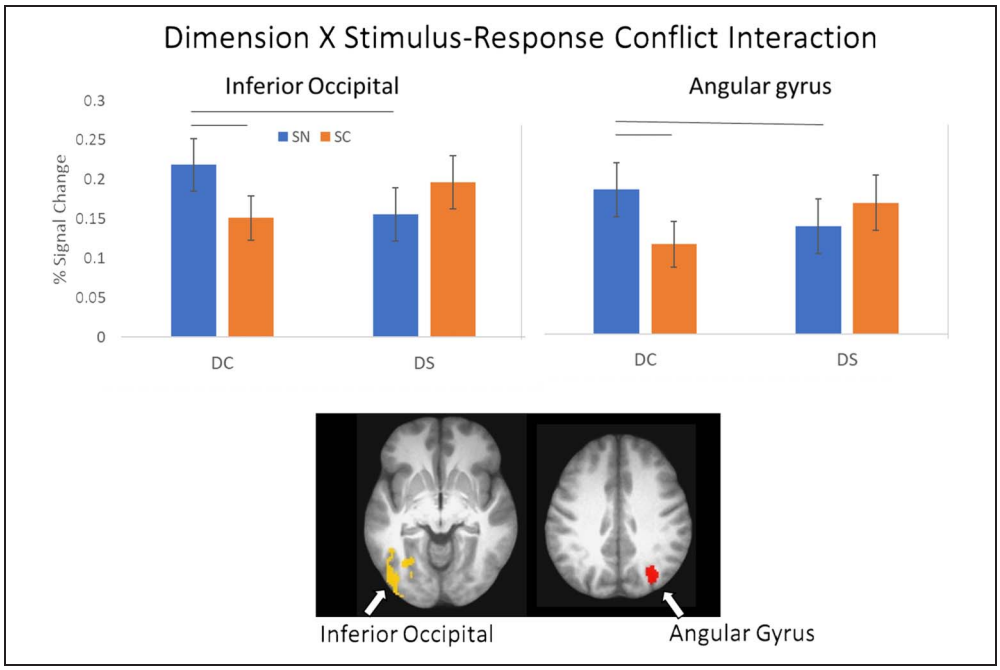

Figure 11. Dimension × SC interaction. Top: average percent signal change from the ROIs showing an interaction between dimension and SC. Error bars represent standard error of the mean. Bottom: location of ROI. See Table 3 for list of ROIs.

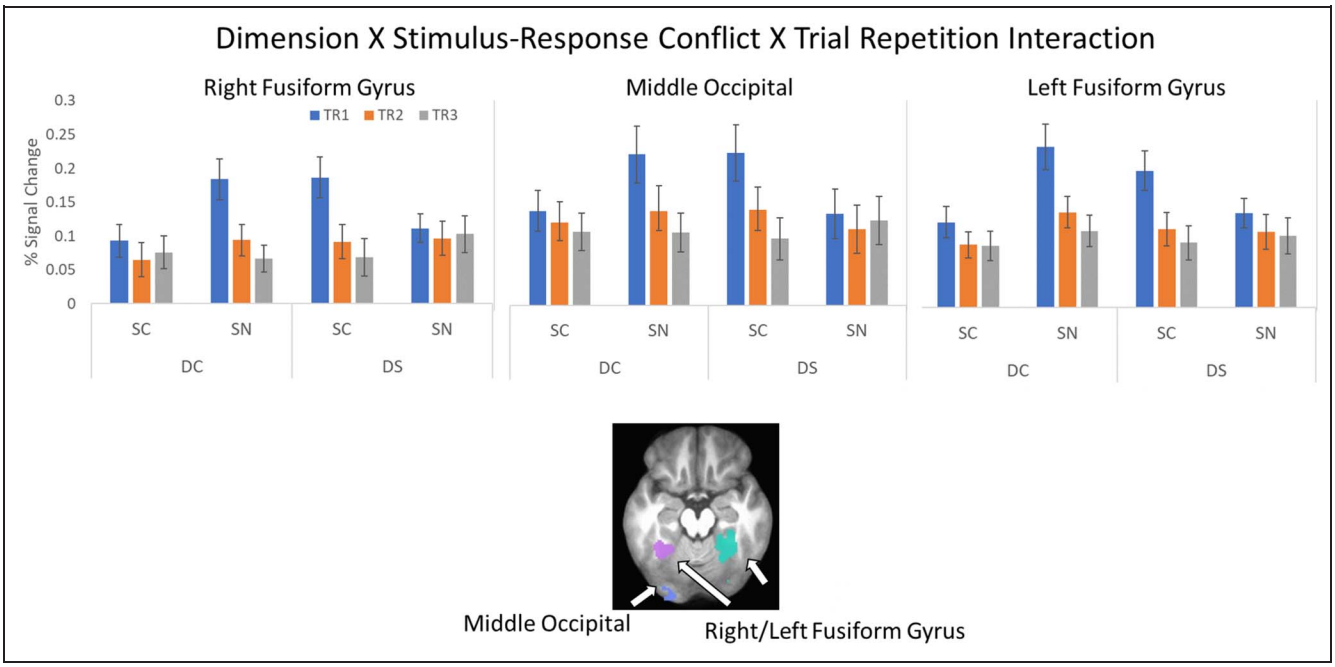

Figure 12. Dimension × SC × Trial Repetition interaction. Top: average percent signal change from the ROIs showing an interaction between dimension, SC, and trial repetition. Error bars represent standard error of the mean. Bottom: location of ROI. See Table 3 for list of ROIs.

higher than on TR3 when the dimension changed ($p < .001$). In addition, activation on TR1 was higher when the dimension changed compared to when it remained the same ($p < .001$; all other $p > .015$). In postcentral gyrus, activation on TR1 was greater when the dimension changed compared to when it remained the same, but the opposite relationship was present on TR3 ($p < .001$; all other $p > .02$). In precuneus, activation was greater on TR1 compared to TR2 ($p = .003$) and on TR2 compared to TR3 when the dimension changed ($p = .002$). In addition, activation on TR1 was greater when the dimension changed compared to when it stayed the same ($p < .001$; all other $p > .094$). Lastly, activation in inferior parietal lobule when the dimension changed was greater on TR1 compared to TR2 and on TR2 compared to TR3 ($p < .001$). In addition, activation when the dimension changed was greater than when the dimension stayed the same on TR1 and TR2 ($p < .001$).

An interaction between Dimension and SC was observed in the left inferior occipital gyrus and right angular gyrus (see Figure 11). In both clusters, activation on DCSN was greater than activation on DSSN and DCSC trials ($p < .005$). Finally, a three-way interaction was observed in the bilateral fusiform gyrus and left middle occipital gyrus (see Figure 12). These regions showed increased activation on TR1 of the DCSN and DSSC conditions (all $p < .0002$).

DISCUSSION

This study presents the first assessment of neural activation in a dimension switching task across multiple types of switch conditions. Specifically, we systematically manipulated the demands on shifting attention to a new dimension and the need to resolve conflict between stimulus–response mappings for the current task and stimulus–response associations from decisions during the previous task. We observed a network of regions that were activated in response to these task demands. First, increased activation on switch trials was observed across a broad network of frontal, temporal, parietal, and subcortical regions. Furthermore, switching attention to a new dimension was associated with increased activation in parietal and frontal regions, whereas the absence of SC was associated with greater activation in fusiform cortex. We also observed an interaction between dimension switching and trial repetitions in parietal cortex and SMA. These regions showed increased activation on switch trials when the task switch involved shifting attention to a new dimension compared to when attention was maintained on the same dimension. An interaction was also observed between the dimension and SC factors in inferior occipital cortex and angular gyrus. These regions displayed increased activation based on the combination of a DC and the absence of feature-conflict. Finally, an interaction between all task factors—dimension, SC, and trial repetitions—was observed in occipital and fusiform cortices. These regions showed a selective increase in activation on switch trials (TR1) during the DCSN and DSSC conditions. This pattern of activation could reflect the additional demands on orienting to the new task set in these conditions. That is, the DCSN condition requires a switch to a new dimension that contains new feature values, whereas in the DSSC condition, the task requires making the opposite spatial response to the same features that were relevant on previous trials.

Taken together, this pattern of results highlights the distinct roles that frontal and posterior brain regions play in flexible dimensional attention. For example, stronger activation was observed in frontal and parietal cortex when the relevant dimension switched compared to when it stayed the same. This suggests that these regions function to shift attention between visual dimensions. This observation is consistent with previous neuroimaging findings with the DCCS (Buss & Spencer, 2018; Ezekiel et al., 2013; Morton et al., 2009). The novel contribution of the data presented here arise from the consideration of the SC factor. First, the main effect of this factor in fusiform cortex showed increased activation in the absence of SC. Second, the SC factor interacted with the DC factor in aspects of occipital and parietal cortex such that increased activation was observed when switching dimensions in the absence of SC. These observations are consistent with the previous observation that reducing SC increases activation in posterior brain regions (Buss & Spencer, 2018). A more complicated picture emerges, however, when considering the three-way interaction of trial repetition, dimension switching, and SC. Three clusters were identified that showed increased activation on switch trials in the diagonal of the interaction between the dimension switching and SC factors—that is, when the dimension changed and SC was absent, or when the dimension stayed the same and SC was present. The latter case is the only situation in which stronger activation was observed in the presence of SC. Thus, in general, activation appears to increase when SC is absent, the one exception being when the task requires a reversal of responses to the same features that were relevant for the previous task.

Across these effects, an intriguing brain–behavior relationship is apparent. Specifically, for the trial repetition and dimension contrasts, stronger activation was observed for trial types that had longer RTs. Typically, such effects in the literature are thought to reflect an enhanced need for cognitive control, that is, between switch and repeat trials or between dimensional change and no change trials. By contrast, the opposite pattern was observed for the SC main effect: Trials that contained SC had longer RTs compared to trials in which SC was absent; however, stronger activation was observed on trials in which SC was absent. In this case, there is a boost in activation in the absence of SC (see also, Buss & Spencer, 2018). Interestingly, we also observed an interaction between SC and dimension switching in occipital cortex. This suggests that this early object representation area is sensitive to both feature-based effects and the need for higher-level cognitive control.

One important limitation of the current study is that the effect of eliminating SC in the SN conditions was achieved by altering the relevant features of the objects. In this regard, it is not clear whether the increased activation in the SN condition relative to the SC condition is because of the elimination of conflict or because of the processing of new features. One alternative way to eliminate SC is to align the response-driven associations from previous decisions with the stimulus–response mappings during the postswitch. For example, if sorting by color in postswitch trials, then the colors involved in the task would be sorted to the same locations during the pre- and postswitch phases (e.g., red is sorted to the left when sorting by shape during the preswitch phase, and red is also sorted to the left when sorting by color during the postswitch phase; see Figure 3). In this way, the memories of previous stimulus–response decision would be supportive of the task mapping required postswitch. Based on the results of Buss and Spencer (2018) who implemented such a condition with 3- and 4-year-olds, we would expect a similar pattern of results to the no-conflict condition in the current study.

It is important to acknowledge the confounds in the current design. These confounds arise from the nature of the task and the constraints placed on how aspects of the task can be manipulated independently. For example, we eliminated the need to switch dimensions by altering the spatial configuration of the task and continuing with the relevant dimension from the previous sorting phase. Thus, the contrast between dimension-same and dimension-change could also be a result of the spatial configuration of the task being altered or remaining the same; however, the regions that were sensitive to this manipulation are consistent with regions involved with dimension switching in previous studies (Ezekiel et al., 2013; Morton et al., 2009). Similarly, we eliminated SC by altering the features of the dimension that was to be relevant for the current phase of sorting. Thus, the regions showing sensitivity to this manipulation could also be a result of the features remaining the same or changing. These limitations, however, can serve to motivate future work exploring these dynamics in the context of the DCCS task. For example, we could compare activation and performance across conditions that require switching dimensions with either the same or altered spatial layout. Relatedly, SC could be manipulated in other ways. For example, activation and performance could be examined when memories from the previous sorting phase cooperate with the configuration of the features for the dimension that is to be relevant for the current sorting phase. This condition would also be absent of SC but would not be confounded with the introduction of new features.

The current data also challenge existing theories of flexible attention. Most theories assume that rule representation is carried out in an abstract manner within regions of frontal cortex (Bunge & Zelazo, 2006; Morton & Munakata, 2002) and response competition processes are resolved in parietal cortex (Crone et al., 2006). That is, the configuration and reconfiguration of rule representations are accomplished by processes in frontal cortex, which exerts a top–down influence on the selection of responses in parietal cortex. This is true also for neurocomputational models that focus on the neurocomputations being carried out by frontal cortex. For example,

Badre and Wagner (2006) describe a computational network in which left ventrolateral frontal cortex involved in "conceptual" conflict, which is dissociated from response conflict in left inferior parietal cortex. Other models have focused on the different functions carried out by frontal cortex, focusing on different types of conflict detection mechanisms (Brown, Reynolds, & Braver, 2007) or the dynamics of updating the representations of task rules in prefrontal cortex via basal ganglia gating mechanism (Herd et al., 2014; Rougier, Noelle, Braver, Cohen, & O'Reilly, 2005). Other models have expanded beyond frontal cortex representations of rules to examine how posterior brain regions are also involved in rule representation processes. A neurodynamic model proposed by Ardid and Wang (2013) does provide a role for visual areas in rule representation processes. Specifically, their model implements neural dynamics involved in dimensional competition and selection in frontal cortex, which enhance processing of visual areas that map stimuli to responses. This model too, though, is not able to account for the effect of stimulus–response associations along the task-irrelevant dimension because this model only forms associations along the task-relevant dimension.

The effects reported here are consistent with a dynamic field model of the development on the DCCS task (Buss & Kerr-German, 2019; Buss & Spencer, 2014, 2018). Similar to the model of Ardid and Wang (2013), the dynamic neural field (DNF) model implements a dimensional attention mechanism that enhances processing of task-relevant visual dimension and representations within the visual dimension provide a mapping of stimuli to responses. In contrast to this model, however, the DNF model is an embodied framework that grounds the processing of visual features in the dynamics of object representation. Building object representations in the DNF model utilizes spatial coupling between visual dimensions to activate the features present on an object. In the context of the DCCS task, the model builds representations of the test object at the selected response location. In this way, the model forms associations between responses and the features of both the relevant and irrelevant dimensions of the objects. Across the behavioral and neural results presented here, there is compelling evidence that response-driven associations form not only along task-relevant dimension but also along the task-irrelevant dimension. This finding stands at odds against most theories of task switching, which posit some form of selective engagement of the task-relevant stimulus features when a task is engaged. From the perspective of the DNF model of flexible attention, however, rule-use reflects the influence of dimensional attention on object representations processes. This framework has been used to explain a wide array of behavioral findings with children in the DCCS (Buss & Kerr-German, 2019; Buss & Spencer, 2014) as well as the quantitative details of neural activation across development and versions of the task that were made easier by virtue response-driven associations distributed across feature dimensions (Buss & Spencer, 2018).

Although the DNF model is consistent at a conceptual level with the results reported here, it is an open question whether the DNF model can quantitatively account for these behavior and neural data. A recent model-based approach to fMRI analyses (Buss et al., 2021; Wijeakumar, Ambrose, Spencer, & Curtu, 2017; Buss, Wifall, Hazeltine, & Spencer, 2014) uses activation from components of the DNF model in the general linear model to predict the BOLD signal. Bayesian multilevel modeling is then used to determine whether the DNF predictors are better than categorical task-based predictors or which components of the DNF model best predict activation across the cortex. This approach can further clarify the functional role that different cortical regions play in flexible attention and the extent to which the DNF model accurately explains patterns of activation.

In summary, the current report provides new insights into the functional role of cortical activation in the context of flexible attention. Our analyses revealed that frontal and parietal cortices help to shift attention from one visual dimension to another and regions of occipital, temporal, and parietal cortex are sensitive to conflict between past stimulus–response bindings and current task demands. Moreover, stimulus–response association accrue along the dimension that is relevant for the current task as well as the dimension that is irrelevant for the current task. This shows how posterior brain regions play a central role in the flexible attention needed to switch between tasks.

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Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were M(an)/M = .408, W(oman)/M = .335, M/W = .108, and W/W = .149, the comparable proportions for the articles that these authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076 (Fulvio et al., *JoCN*, 33:1, pp. 3–7). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

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